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Temperature-mediated functional response of *Theocolax elegans* (Hymenoptera: Pteromalidae) parasitizing *Rhyzopertha dominica* (Coleoptera: Bostrichidae) in stored wheat

P.W. Flinn*, D.W. Hagstrum

Grain Marketing and Production Research Center, USDA, ARS, 1515 College Avenue, Manhattan, KS 66502, USA

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Abstract

The functional response of *Theocolax elegans* (Westwood) parasitizing the lesser grain borer, *Rhyzopertha dominica* (F.) was examined over a range of temperatures. A type II functional response equation was fitted to each temperature regime. The parasitization rate was highest at 30°C (20 hosts per day) and was lowest at 20°C (2 hosts per day). Handling time was inversely proportional to temperature, and ranged from 1.6 days at 20°C to 0.05 days at 30°C. Instantaneous search rate also changed with temperature. It was lowest at 20°C and highest at 30°C. A temperature-mediated functional response equation was fitted to the data, in which handling time was a quadratic function of temperature. The equation explained 74% of the variance in parasitization rate. *Theocolax elegans* has a narrower optimal temperature range than other parasitic stored-product Hymenoptera. Temperatures greater than 32.5°C caused high parasitoid mortality. Published by Elsevier Science Ltd.

Keywords: *Rhyzopertha dominica*; Parasitoid; *Theocolax elegans*; Biological control; Functional response; Model; Stored grain

1. Introduction

The lesser grain borer, *Rhyzopertha dominica* (F.), is one of the most common and damaging insect pests of stored wheat in the United States. The immature stages develop inside the wheat kernel. This insect is one of the major causes of insect contamination in flour because the immature stages and pre-emergent adults cannot be removed from the wheat before it is milled.

*Corresponding author. Tel.: +1-785-776-2707; fax: +1-785-537-5584.

E-mail addresses: flinn@usgmrl.ksu.edu (P.W. Flinn).

Theocolax elegans (Westwood) is a cosmopolitan pteromalid wasp that parasitizes *Rhyzopertha dominica*. It also parasitizes other stored grain beetles such as the curculionids *Sitophilus oryzae* (L.), *S. granarius* (L.), and *S. zeamais* Motschulsky. This wasp only parasitizes larvae that are feeding inside the grain kernel (van den Assem and Kuenen, 1958). On *S. zeamais*, the female prefers to parasitize pupae and 4th-instar larvae (Sharifi, 1972). They normally lay one egg externally on each host. The life cycle is about 22 days at 27°C (Sharifi, 1972). The females live for 2–3 weeks (van den Assem and Kuenen, 1958). This wasp has been effective in reducing populations of *S. zeamais* by up to 50% in field experiments (Williams and Floyd, 1971).

Theocolax elegans adults are very small (1–2 mm), and do not feed on the grain. They normally die within 5–10 days if no hosts are present in the grain. Because the adult wasps are external to the grain, they can easily be removed from it using normal cleaning processes. These parasitoids are found naturally in stored grain, which suggests that once released they may continue to suppress pests for many years.

The rate at which parasitoids attack hosts is dependent on host density. This relationship has been described as a functional response to host density (Solomon, 1949). Temperature also affects functional response, and general models have been developed (Mack et al., 1981; Flinn, 1991). This paper presents a temperature-mediated functional response for *T. elegans* parasitizing the lesser grain borer, *R. dominica*.

2. Materials and methods

All insects used in this study were obtained from cultures maintained at the Grain Marketing and Production Research Center in Manhattan, KS, and were originally derived from local collections. The *T. elegans* culture was approximately one year old; the age of the *R. dominica* culture was unknown. One- to two-day-old eggs of *R. dominica* were obtained by allowing adults to oviposit in flour, and then sieving the flour to recover the eggs. Because we needed to recover the infested kernels after the 24 h parasitization period, white wheat kernels were used. The white wheat kernels are slightly lighter in color than hard red winter wheat; this allowed us to recover the infested kernels after they were mixed into the hard red winter wheat. The white wheat kernels were infested with *R. dominica* larvae by using a needle to make a small hole in the kernel, and placing one *R. dominica* egg on it. The kernels were placed into individual vials and held at 30°C for 20 days to allow them to develop into the 4th instar. Either 0, 2, 4, 8, or 16 infested kernels were mixed into 330 g of hard red winter wheat (12% moisture content, wet weight). The wheat was put into glass jars (7 cm diameter, 13.5 cm tall) and each jar was covered with filter paper. Newly emerged female *T. elegans* were kept with males for 24 h and then placed into the jars. The jars were placed into chambers held at either 20, 25, 30, or 32.5°C for 24 h; there was no photoperiod and the relative humidity in the chambers was maintained at $65 \pm 5\%$. We did not test 35°C because a previous experiment showed that *T. elegans* could not develop at this temperature. After 24 h, the infested kernels were recovered from the grain and placed into individual vials. The vials with the infested kernels were held at 30°C for 15 days to determine if the infested kernels were parasitized (*R. dominica* adults emerged from unparasitized kernels, adult wasps emerged from parasitized kernels).

A type II equation for parasitoids (Royama, 1971) was used to estimate instantaneous search rate and handling time, for each temperature, using a nonlinear procedure (SYSTAT, 1999):

$$N_p = N_t \left\{ 1 - \exp \left\{ - \frac{aTP_t}{1 + aT_h N_t} \right\} \right\}, \quad (1)$$

where N_p is the number of hosts parasitized, N_t is the number of hosts available, a is the instantaneous search rate, T is the duration of the experiment in days, P_t is the number of parasitoids, and T_h is the parasitoid handling time.

A temperature-mediated functional response model (Flinn, 1991) was used to predict the functional response over a range of temperatures by substituting a quadratic function for T_h :

$$N_p = N_t \left\{ 1 - \exp \left\{ - \frac{aTP_t}{1 + a(B_0 - B_1X + B_2X^2)N_t} \right\} \right\}, \quad (2)$$

where X is the temperature in centigrade, and the other parameters are as previously defined. This four parameter equation was fitted to the data using a nonlinear procedure (SYSTAT, 1999) to estimate a , B_0 , B_1 and B_2 .

3. Results and discussion

The Royama (1971) equation was fitted to each temperature separately (Table 1). Parasitization increased with host density at all of the temperatures tested, and was similar to a type II functional response (Holling, 1965). There was a high amount of variability in parasitization among wasps; this reduced the r^2 values. All of the regressions were significant ($P < 0.01$) except for 20°C. The slope of this line was very flat, which resulted in low r^2 and P values. However, the regression at 20°C is still important because it shows that *T. elegans* has a very low parasitization rate at this temperature. Instantaneous search rate, a , changed with temperature; it was lowest at 20°C and reached a maximum at 25°C. Handling time, T_h , also varied with temperature. It was longest at 20°C, and shortest at 30°C. The predicted maximum number of parasitized larvae in 1 day ($1/T_h$) was highest at 30°C (20 larvae/day). At 32.5°C, the rate of parasitization was less than at 30°C. At 35°C all of the wasps died after 24 h. Fig. 1 shows the equation fitted to each temperature. The rate of parasitization was more variable at 30 and 32.5°C than at 25°C.

Table 1

Estimate of instantaneous search rate, a , and handling time, T_h , for Royama's functional response equation for parasitoids

Temperature (°C)	N	a (day ⁻¹) ± SE	T_h (day) ± SE	r^2	P	Max. no. parasitized
20.0	20	0.007 ± 0.014	1.57 ± 7.47	0.15	0.33	0.6
25.0	20	0.32 ± 0.174	0.19 ± 0.06	0.80	<0.01	5.5
30.0	34	0.219 ± 0.069	0.05 ± 0.04	0.82	<0.01	20.0
32.5	20	0.150 ± 0.104	0.06 ± 0.12	0.62	<0.01	17.1

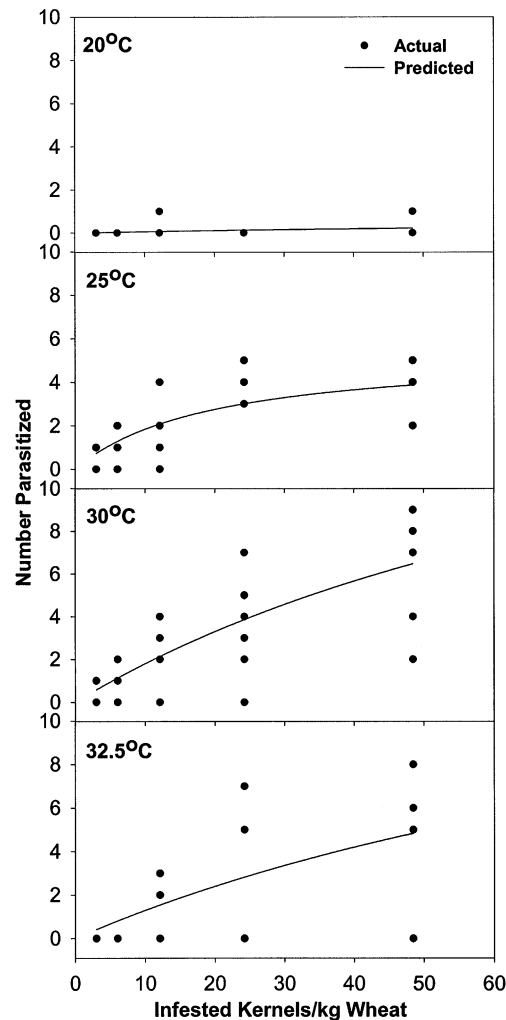


Fig. 1. Functional response of *Theocolax elegans* parasitizing the lesser grain borer, *Rhyzopertha dominica*, at four different temperatures. A type II functional response equation was fitted separately for each temperature.

Because we wanted to predict the functional response of *T. elegans* over a range of temperatures, we fitted a temperature-mediated functional response equation to the data (Eq. (2)). In this equation, a quadratic function, that included temperature, was substituted for T_h . We used a quadratic function because we noted that T_h reached a minimum value at 30°C and was larger at higher and lower temperatures (Table 1). Estimates and standard errors for a , B_0 , B_1 and B_2 were 0.211 ± 0.050 , 7.21 ± 2.08 , -0.490 ± 0.144 , and 0.008 ± 0.003 , respectively. Eq. (2) fitted the data well ($r^2 = 0.74$, $N = 93$, $P < 0.01$). Fig. 2 shows a graph of the predicted functional response of *T. elegans* over a range of temperatures. The optimal temperature for high rates of parasitization was 30°C. We also fitted a six-parameter equation (not shown) in which both instantaneous search rate and handling time were quadratic functions of temperature ($r^2 = 0.76$; $N = 93$, $P < 0.01$).

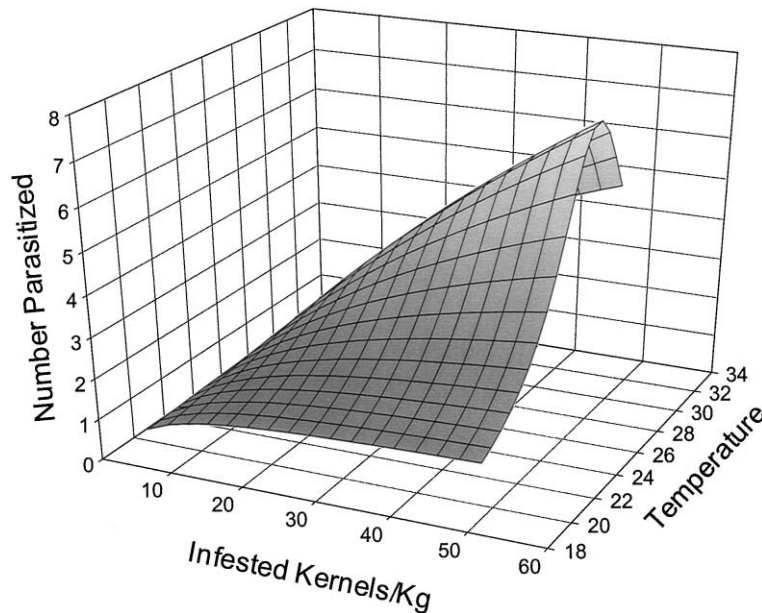


Fig. 2. Temperature-mediated functional response (Eq. (2)) of *Theocolax elegans* parasitizing the lesser grain borer, *Rhyzopertha dominica*.

Because the r^2 value was only slightly higher for the six-parameter model, Eq. (2) was selected as the best model.

Theocolax elegans appears to have a narrower temperature range for optimal parasitization than other stored-grain parasitoids such as *Cephalonomia waterstoni* (Gahan) and *Anisopteromalus calandrae* (Howard). For example, *C. waterstoni* is able to parasitize up to 3 larvae/12 h at both 20 and 38°C (Flinn, 1991). *Anisopteromalus calandrae* parasitizing *Sitophilus zeamais* in corn is able to parasitize approximately 1 larva/day at 20°C and 8 larvae/day at 35°C (Smith, 1994). At 30°C, the estimated instantaneous search rate for *A. calandrae* was 1.33 (Smith, 1994); this is considerably higher than our estimate of instantaneous search rate for *T. elegans*. However, the handling time for *A. calandrae* at 30°C was 0.13, while the handling time for *T. elegans* was 0.05. A lower handling time means higher numbers of hosts can be parasitized in a given time interval. Thus, it appears that *A. calandrae* may be more efficient at attacking hosts at low densities, but that *T. elegans* may be able to parasitize greater numbers of hosts at high host densities. These differences, however, could be due to host differences and/or media differences (wheat vs. maize).

For *T. elegans* to be effective in suppressing *R. dominica*, it may be necessary to cool the grain to temperatures below 30°C as soon as possible using aeration. This would also have the beneficial effect of suppressing *R. dominica* development in stored grain. In a laboratory experiment, Flinn (1998) showed that *T. elegans* was ten times more effective at suppressing populations of *R. dominica* in grain that was cooled to 25°C, than in grain that was held at 32°C. The reason for this difference may be due to a combination of two factors: (1) the population growth rate of *R. dominica* is reduced by half at 25°C compared to 32°C; and (2) the functional response of *T. elegans* parasitizing *R. dominica* is almost the same at 25 and 32°C.

Information from this study will be used to develop a host-parasitoid model of *T. elegans* parasitizing *R. dominica*. This model should enhance our ability to develop biological control programs for stored grain.

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